
New Species and Combinations in *Physaria* (Brassicaceae) from Western North America

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ABSTRACT. Three new species of *Physaria* (Nuttall) A. Gray from the western United States are described and illustrated: *P. eriocarpa* Grady & O’Kane, *P. pachyphylla* O’Kane & Grady, and *P. pycnantha* Grady & O’Kane. *Physaria curvipes* (A. Nelson) Grady & O’Kane and *P. spatulata* (Rydberg) Grady & O’Kane are proposed as new combinations in the genus and are provided with updated descriptions. Taxonomic changes are the product of a molecular study of these species and others formerly allied with *P. reediana* O’Kane & Al-Shehbaz (= *Lesquerella alpina* (Nuttall) Watson). A key is provided that includes the species described here as well as other central Rocky Mountain species traditionally affiliated with *P. reediana*.

Key words: Brassicaceae, Canada, *Lesquerella*, *Physaria*, United States.

The taxonomy of the species in the genus *Physaria* (Nuttall) A. Gray (which includes most of the species formerly included in *Lesquerella* S. Watson) has undergone revision several times over the past century (Payson, 1921 [1922]; Rollins & Shaw, 1973; Rollins,

1993; Al-Shehbaz & O’Kane, 2002). Some species groups within the genus have been especially problematic. Species historically associated with *P. reediana* O’Kane & Al-Shehbaz (= *Lesquerella alpina* (Nuttall) Watson) are one such group. In the past, one polymorphic species or as many as seven species have been informally included in the *P. reediana* species complex (Rollins & Shaw, 1973). Recently, a molecular analysis of the evolutionary history of this difficult group of species was performed to clarify its relationships and taxonomy (Grady, 2005). The presence of more taxa than formerly recognized in this complex is not surprising. The genus *Physaria* is speciose in the western United States and contains many local and edaphic endemics (Rollins & Shaw, 1973). Since Rollins’ (1993) treatment of the Brassicaceae in North America, seven new species of *Physaria* have been discovered in the western United States (e.g., Rollins, 1995; Rollins et al., 1995; Anderson et al., 1997; O’Kane, 1999; O’Kane & Reveal, 2006). We propose three additional new species and two new combinations in *Physaria* based on field, herbarium, and molecular studies.

KEY TO THE NORTH AMERICAN SPECIES PREVIOUSLY OR CURRENTLY ASSOCIATED WITH *PHYSARIA REEDIANA*

- 1a. Rays of trichomes closely appressed to surface of mature silicle.
 - 2a. All basal leaves linear, 1–1.5 mm wide; north-central Colorado and the Uinta Mtns. of Utah and Wyoming
..... *P. parvula* (Greene) O’Kane & Al-Shehbaz
 - 2b. Basal leaves spatulate to orbicular or rhombic in outline, wider than 2 mm, to 8 mm.
 - 3a. Basal leaves rhombic in outline, leaf blade distinct from petiole, almost always folded; silicles as wide as long (2–4 mm), styles to 2 mm, shorter than mature silicles; northwest Colorado, northeast Utah, and southwest Wyoming
..... *P. subumbellata* (Rollins) O’Kane & Al-Shehbaz
 - 3b. Basal leaves spatulate to nearly orbicular in outline, not folded; silicles larger (3.5 mm or greater), usually longer than wide; distribution elsewhere.
 - 4a. Styles noticeably longer than silicles; plants caespitose, fruiting stems to 5 cm, never more than 2 × longer than basal leaves; basal leaves mostly narrowly oblanceolate, blade gradually narrowed to petiole; northern Colorado and southwest Nebraska, then northwest through central Wyoming
..... *P. reediana* (Nuttall ex Torrey & A. Gray) O’Kane & Al-Shehbaz
 - 4b. Styles to 6 mm, roughly equal to or shorter than length of silicles; plants loose, not caespitose, fruiting stems to 24 cm, often much longer than basal leaves; blade abruptly narrowed to petiole in outer basal leaves.
 - 5a. Fruiting pedicels curved; basal leaves nearly 1 mm thick, blades cupped; silicles globose with acute apices, densely covered by trichomes; Pryor Mtn. desert of south-central Montana
..... 3. *P. pachyphylla* O’Kane & Grady
 - 5b. Fruiting pedicels sharply sigmoid; basal leaves not thickened, blades flat; silicles ellipsoid with acute apices, sparsely covered by trichomes.
 - 6a. Fruiting pedicels 2 × long or longer (10–20 mm) than mature silicles; styles ± equal to silicles in length, to 6 mm; plants widespread, from western Nebraska and Wyoming

- northward to southern Alberta and Saskatchewan . . . 5. *P. spatulata* (Rydberg) Grady & O'Kane
- 6b. Fruiting pedicels less than $2 \times$ length (4–7 mm) of mature silicles; styles shorter than mature silicles (1.5–2.5 mm long); plants limited to the Big Horn Mtns., Wyoming and Montana 1. *P. curvipes* (A. Nelson) Grady & O'Kane
- 1b. Rays of trichomes long (up to 0.5 mm), erect or ascending, giving the mature silicles a shaggy appearance.
- 7a. Basal leaves narrowly obovate to suborbicular, folded, blade abruptly narrowed to petiole; caudex thickened, \pm 1 cm; Sheep Mtn. in the Pioneer Range of southwest Montana 2. *P. eriocarpa* Grady & O'Kane
- 7b. Basal leaves linear to oblanceolate, no distinction between blade and petiole; caudex narrow, only to 5 mm width; distribution elsewhere.
- 8a. Styles longer than mature silicles, to 4 mm; fruiting stems never exceeding basal leaves; trichomes once bifurcate, not fused near base; southwest Wyoming. *P. nelsonii* (A. Nelson) O'Kane & Al-Shebaz
- 8b. Styles shorter than silicles, only to 3 mm; fruiting stems often longer than basal leaves, to 7 cm; trichomes twice bifurcate, fused less than 10% of ray length at base; east-central Idaho and southwest Montana 4. *P. pycnantha* Grady & O'Kane

1. *Physaria curvipes* (A. Nelson) Grady & O'Kane, comb. nov. Basionym: *Lesquerella curvipes* A. Nelson, Bull. Torrey Bot. Club 25: 205. 1898. TYPE: U.S.A. Wyoming: Dome Lake Grade, A. Nelson 2424 (holotype, RM; isotypes, GH, NY). Figure 1.

Loosely spreading perennial; caudices singular, 2–3 mm diam.; stems usually decumbent, well exerted beyond basal leaves, 8–24 cm, often red-purple in color. Basal leaves erect, spatulate to nearly rhombic, $25\text{--}50(-90) \times 2\text{--}4(-6)$ mm, blade gradually narrowed to the petiole; leaves covered by stellate trichomes, 0.3 mm diam., 4 or 5 main rays, once to twice bifurcate, slightly fused near bases, tuberculate, 16 to 24 terminal rays, closely appressed to leaf surfaces; cauline leaves few, spatulate. Inflorescence racemose, pedicels curved-ascending to sigmoid, 4–7 mm. Sepals pale yellow, 3.5–4 mm, pubescent; petals yellow, ligulate, 4–6 mm; ovules 2 to 4 per locule; styles glabrous, 1.5–2.5 mm. Silicles ellipsoid, not inflated, strongly flattened parallel to the septum, apical constriction evident, $(3\text{--})5\text{--}9$ mm \times 2–4 mm; silicle trichomes closely appressed to surface, valve interiors glabrous; styles never more than half of the length of the mature silicles.

Physaria curvipes (curved bladderpod) was first recognized by Aven Nelson in 1898 as *Lesquerella curvipes* A. Nelson. Rollins and Shaw (1973) thought that this species represented a form of the highly variable *L. alpina* subsp. *alpina* (Nuttall) Rollins & Shaw, and thus *L. curvipes* was reduced to synonymy. The close relationship of *P. curvipes* and *P. reediana* is apparent from recent molecular work (Grady, 2005). Morphologically, *P. curvipes* is distinct from *P. reediana*, and their primary ranges do not overlap.

Physaria curvipes is a perennial species, endemic to the Big Horn Mountains in Wyoming and Montana (Fig. 2). Like many other members of the genus, it is associated with soils derived from limestone parent material and can inhabit areas of high solar intensity

(pers. obs.). The species has a broad elevation range of 1650–2775 m above sea level. It is interesting to note the loose growth form of *P. curvipes* present at such elevations, because other members of the genus, e.g., *P. humilis* (Rollins) O'Kane & Al-Shehbaz, occurring at the upper end of this elevation gradient are typically densely caespitose.

Physaria curvipes can be distinguished from *P. reediana* by silicle, pedicel, and basal leaf shape, as well as growth form. *Physaria curvipes* has silicles that are larger (usually 5–9 mm) and strongly flattened parallel to the septum (Fig. 1), whereas the silicles of *P. reediana* are smaller (3.5–5 mm) and are nearly terete. The fruiting pedicels of *P. curvipes* are often sharply sigmoid, while the pedicels of *P. reediana* are curved-ascending. *Physaria curvipes* has basal leaves that are narrowly spatulate to nearly rhombic (to 90 mm long) and a loose growth habit; *Physaria reediana* has basal leaves that are lanceolate in outline and has a more compact growth form. *Physaria curvipes* is limited to the Big Horn Mountains in north-central Wyoming and south-central Montana. *Physaria reediana* can be found in northwest Nebraska, north-central Colorado, and southeast and central Wyoming, in the United States.

Physaria curvipes superficially resembles *P. spatulata* (Rydberg) Grady & O'Kane, but the two species are not directly related. Both taxa exhibit loose growth forms and sigmoid-curved fruiting pedicels. They can best be differentiated by fruiting pedicel length and style length. *Physaria curvipes* has pedicels that range from 4–7 mm in length, while the pedicels of *P. spatulata* are longer, ranging from 10–20 mm. The styles of *P. curvipes* are never more than half the length of mature silicles, while the styles of *P. spatulata* are often equal to the length of the mature silicles. The silicles of *P. curvipes* are larger (usually 5–9 mm) and more flattened than those of *P. spatulata*. Thus, in *P. curvipes* the pedicels are 4–7 mm and less than two times longer than the silicles, while in *P. spatulata* the pedicels are 10–20 mm and

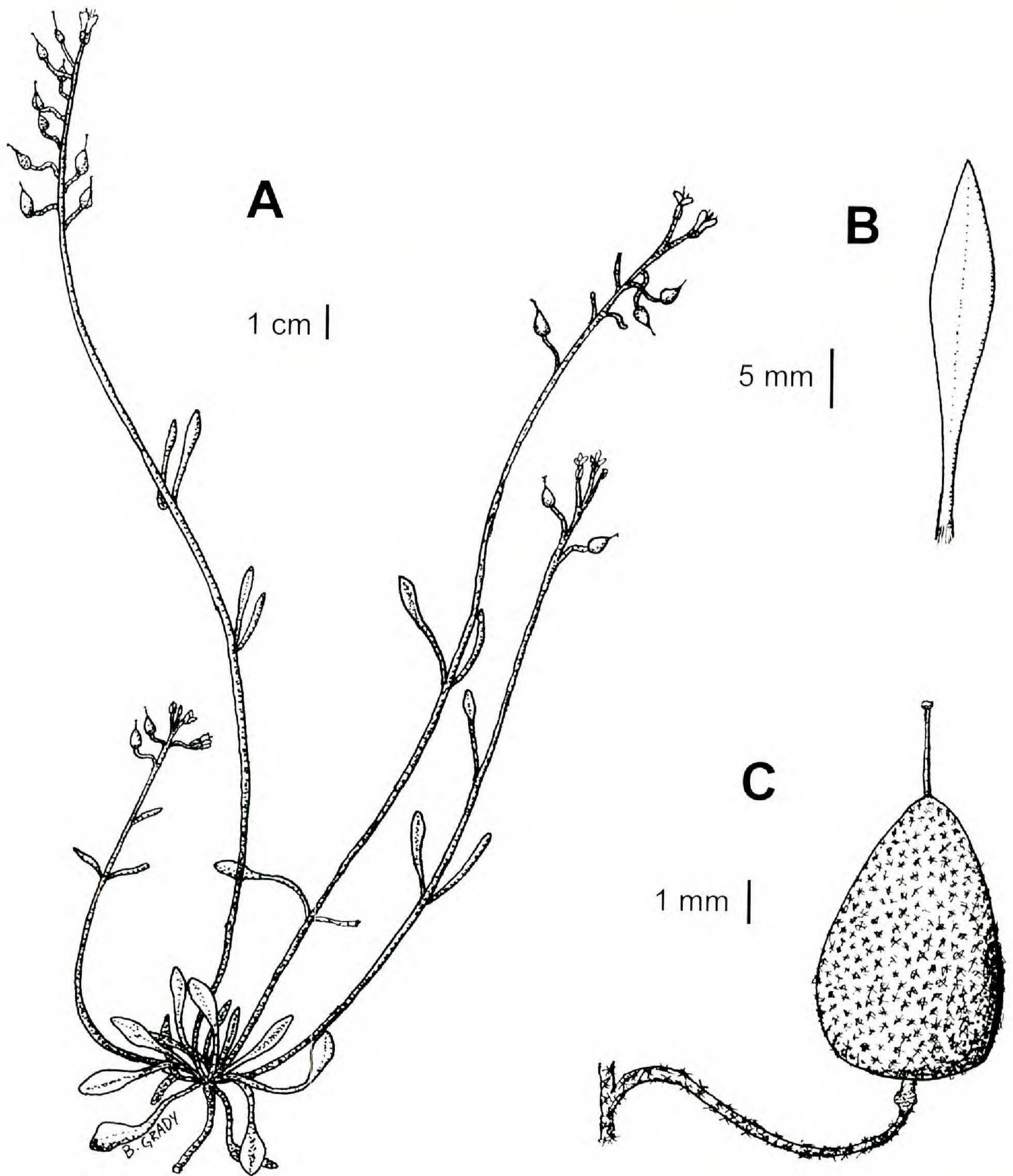


Figure 1. *Physaria curvipes* (A. Nelson) Grady & O'Kane. —A. Plant (pressed). —B. Basal leaf. —C. Silicle and fruiting pedicel. Drawn from *Dueholm* 6667 (NY).

over two times longer than the silicles. The combination of short pedicels, short styles, and large silicles gives the infructescences of *P. curvipes* a distinct appearance compared to those of *P. spatulata*.

Representative specimens examined. U.S.A. **Montana:** Big Horn Co., Big Horn Mtns., limestone gravelly soil on Big Horn divide ca. 1 mi. S of Windy Point Lookout, *P. Lesica* 1029 (MONTU). **Wyoming:** Sheridan Co., 8 mi. E of WYarno, *Dueholm* 6667 (NY); Sheridan Co., 6 mi. W of Dayton on Hwy. 14, steep shaley, limy roadcut in ponderosa pine zone, Amsden Formation, *S. L. O'Kane Jr. & B. R. Grady* 7903 (GH, ISTC, MO); Big Horn Mtns. at summit of Forest Rd. 144, NE of Baldy Pass, alpine meadow, cobbly-gravelly soil of white limestone on windy ridge, *S. L. O'Kane Jr. & B. R. Grady* 7905 (GH, ISTC, MO, NY, RM); steep

hillside near the mouth of Big Goose Canyon, E base of the Big Horn Mtns., *R. C. Rollins* 443 (GH); Dayton Grade, ca. 6 mi. W of Dayton, steep loose limy bank, *R. C. Rollins* 57181 (B, BM, CS); Big Horn Co., limestone benches overlooking Big Horn Valley, turnout in US Hwy. 14A, SW of summit of Limestone Mtn., *B. C. Johnston & P. Lucas* 1839 (COLO); Big Horn Mtns., 13.8 mi. E of Shell on Hwy. 14 in Shell Creek Canyon, steep limy roadcut, *B. R. Grady* 68 (ISTC, MO, RM).

2. *Physaria eriocarpa* Grady & O'Kane, sp. nov.
 TYPE: U.S.A. Montana: Beaverhead Co., ridge-line betw. Sheep Mtn. & Black Lion Mtn., windswept ridge at limber pine krummholz, vegetation sparse & mostly mat-forming, pure

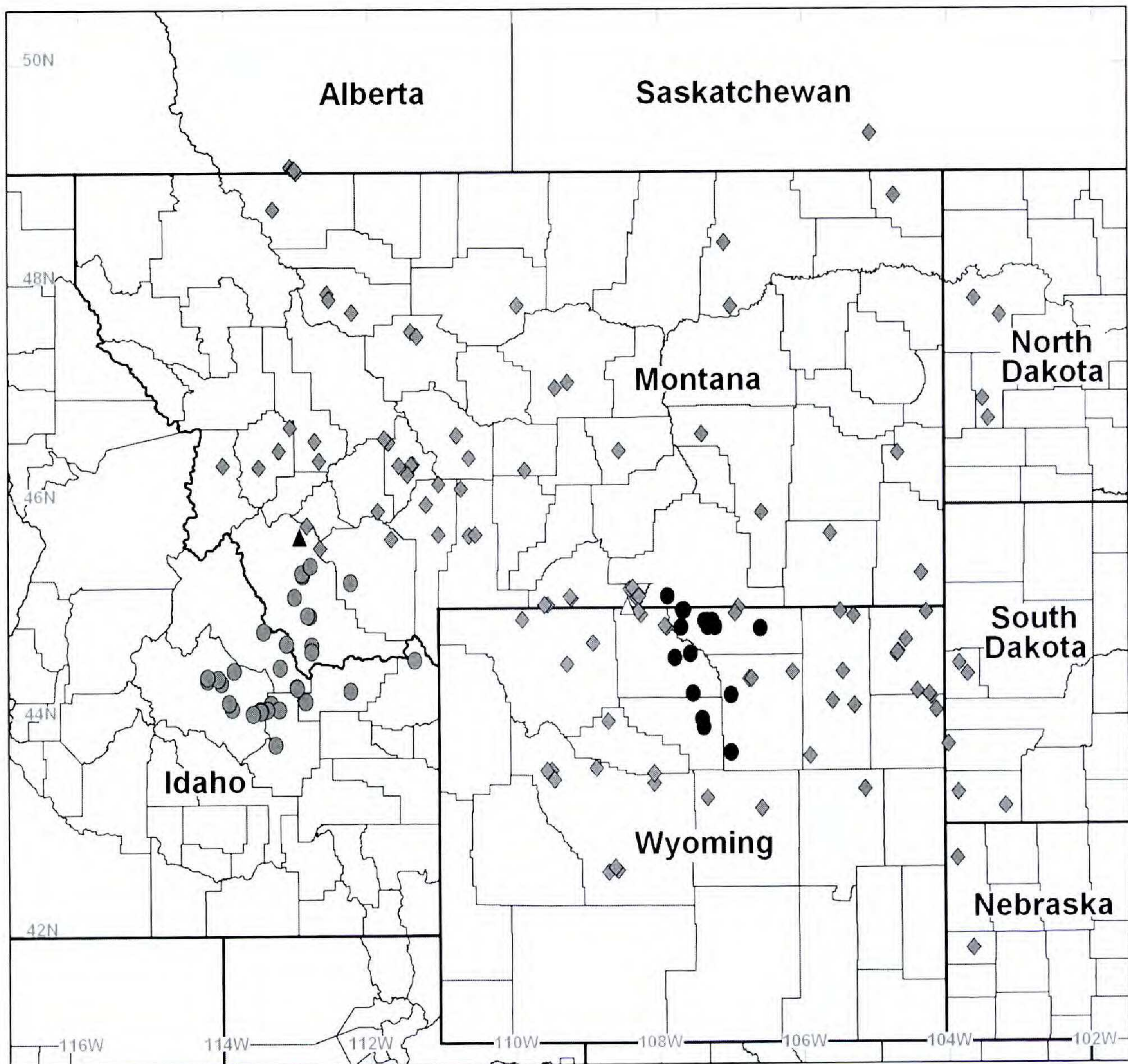


Figure 2. Distribution of new species and combinations of *Physaria* presented here: *P. curvipes* (black circle), *P. eriocarpa* (black triangle), *P. pachyphylla* (white triangle), *P. pycnantha* (gray circle), and *P. spatulata* (gray diamond).

white limestone gravel & cobbles, 8700 ft., 23 July 2005, S. L. O'Kane Jr. & B. R. Grady 7927 (holotype, GH; isotypes, BRY, COLO, ISTC, MO, MONT, MONTU, NY, RM, UTC). Figure 3.

Haec species ad *Physariam nelsonii* (A. Nelson) O'Kane & Al-Shebaz maxime accedit, sed ab ea foliorum basalium lamina obovata orbicularive valde plicata ex petiolo distincta, caule fructifero ex foliis basalibus bene exserto atque siliqua ovoidea ellipsoideave distinguitur.

Long-lived perennial, caespitose, caudex thickened, (4–)8–11 mm, branched; stems well exserted beyond basal leaves, 3.5–9(–12) cm long. Basal leaves erect, 15–25 × 3–8 mm, entire, blade obovate to orbicular, evidently distinct from petiole, folded; leaf trichomes ca. 0.7 mm diam., tuberculate, 5 or 6 main rays, slightly fused at base, 18 to 22 terminal rays; cauline leaves few, spatulate. Inflorescence racemose; pedicels curved-ascending to slightly sigmoid, 5–8 mm. Sepals pale yellow, 4–5 mm,

pubescent; petals yellow, ligulate, 6–7 mm, glabrous; styles glabrous, 4–5 mm; ovary with 4 ovules per locule. Silicles ovoid to ellipsoid, slightly inflated, 2.5–3.5 × 2–3 mm, not compressed at apex, styles longer than silicles; rays of trichomes erect on surface of mature silicles giving fruit shaggy appearance.

Physaria eriocarpa (Sheep Mountain bladderpod) is a compact perennial species with an extremely limited distribution. It is known only from the summit and adjacent ridges of Sheep Mountain in the Pioneer Range of southwestern Montana (Fig. 2). This area was visited by Grady in June 2004 and again by both authors in July 2005. The 2004 collection (Grady 61) was made prior to the onset of flowering. *Physaria pulchella* (Rollins) O'Kane & Al-Shebaz and *P. spatulata* were found flowering and in fruit at lower elevations in the Pioneer Range at the same time. The 2005 visit occurred over a month later in the growing season, and many plants at the type locale were found

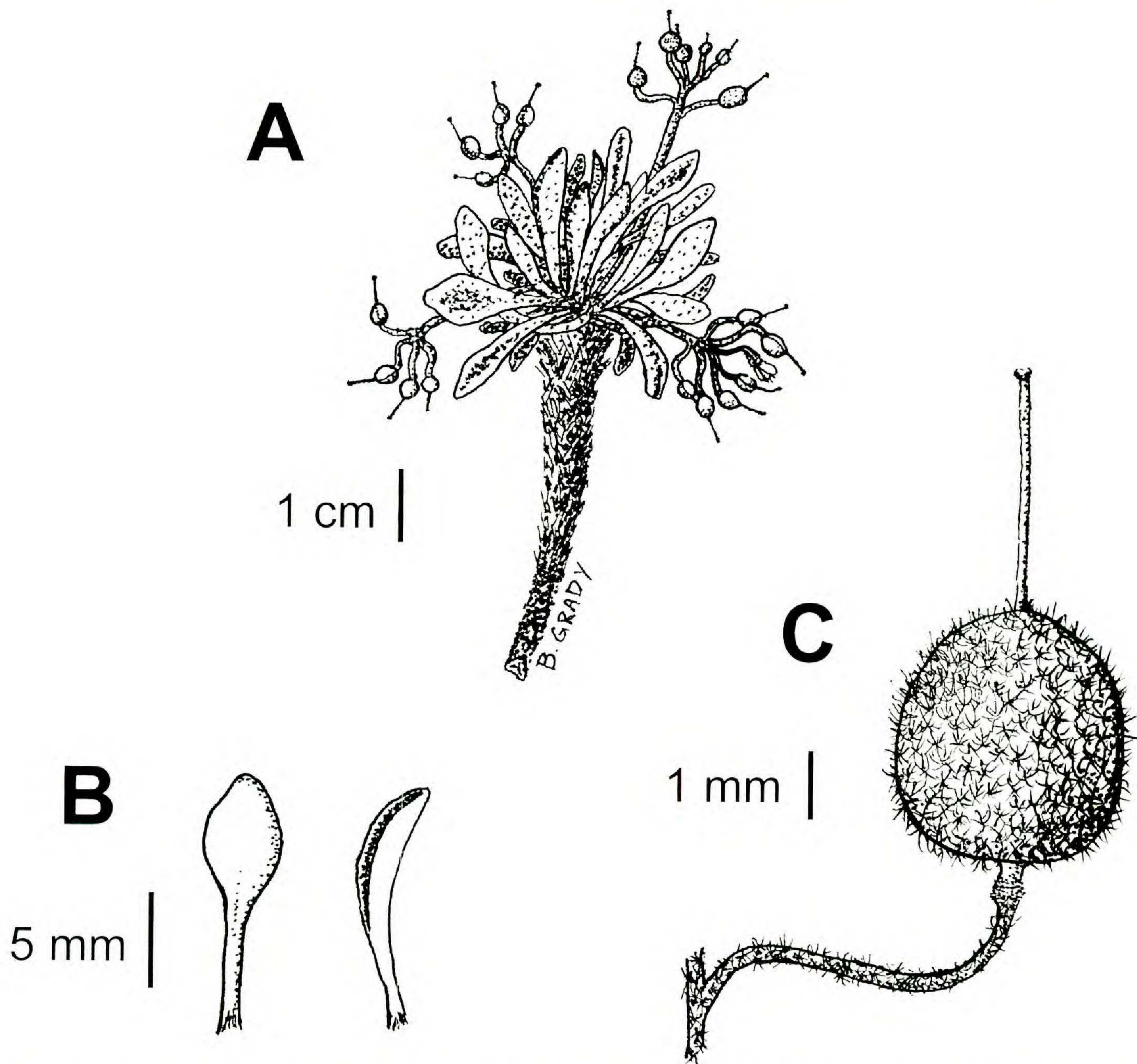


Figure 3. *Physaria eriocarpa* Grady & O'Kane. —A. Plant (pressed). —B. Basal leaf. —C. Silicle and fruiting pedicel. Drawn from the holotype, O'Kane & Grady 7927 (GH).

with both flowers and fruit (O'Kane & Grady 7927, holotype; O'Kane & Grady 7930). With the exception of the collections made by the authors, *P. eriocarpa* has been collected on only one other occasion (C. L. Hitchcock & C. V. Muhlick 12950) but was identified as *Lesquerella condensata* A. Nelson (= *Physaria nelsonii*) due to similarities in morphology. The recent phylogenetic analysis, based on molecular and morphological data, supports a close relationship between the two taxa (Grady, 2005), but *P. eriocarpa* and *P. nelsonii* are clearly distinct species. Both species are densely caespitose, and the plants appear silvery due to a thick covering of stellate trichomes. The silicles of *P. eriocarpa* and *P. nelsonii* appear shaggy because the rays of the trichomes are long, up to 0.5 mm, and erect; also the styles are noticeably longer than the mature silicles in both species. The two species can be distinguished by basal leaf shape,

silicle shape, and stem length. *Physaria eriocarpa* has obovate to orbicular basal leaf blades that are distinct from the petioles and are also strongly folded (15–25 mm). The basal leaves of *P. nelsonii* are shorter overall (5–15 mm), oblanceolate in outline, and the blade gradually narrows to the petiole. The mature silicles of *P. eriocarpa* are not apically compressed, while the silicles of *P. nelsonii* show strong apical compression in both planes. Fruiting stems in *P. eriocarpa* are long (3.5–9 cm) and exerted well beyond the basal leaves. All *P. nelsonii* specimens examined, as well as all individuals observed in the field, exhibited fruiting stems that were concealed within the basal leaves. The ranges of these two species do not overlap and are geographically separated by ca. 320 km.

Physaria eriocarpa is easily distinguished from other species of *Physaria* occurring in nearby areas.

Physaria pulchella is a narrow endemic of the Pioneer Mountains and adjacent areas in Montana and Idaho. The silicles of *P. pulchella* are strongly compressed contrary to the septum (Rollins, 1995), while the silicles of *P. eriocarpa* show no plane of compression. *Physaria spatulata*, a broadly distributed species, is also known from the Pioneer Range. Its silicles show strong apical compression and have trichomes that are closely appressed to the surface of mature silicles. *Physaria eriocarpa*, as mentioned before, has silicles that are not apically compressed, and the rays of the trichomes are long, up to 0.5 mm, and erect, giving the silicle a shaggy appearance. *Physaria eriocarpa* can be distinguished from *P. pycnantha* Grady & O'Kane by the shape of the basal leaves and the shape of the silicles. The basal leaves of *P. pycnantha* are nearly linear to spatulate and show no distinction between blade and petiole; the silicles also exhibit apical compression.

Paratypes. U.S.A. **Montana:** Beaverhead Co., Pioneer Mtns., summit of Sheep Mtn., windswept alpine fellfield of limestone cobbles, 23 July 2005, S. L. O'Kane Jr. & B. R. Grady 7930 (GH, ISTC, MO, RM); Pioneer Mtns., S of Dewey, crest of limy ridge betw. Sheep & Black Lion Mtns., off hiking trail, ca. 2 mi. from trailhead, 17 June 2004, B. R. Grady 61 (ISTC); on high limestone ridge connecting Sheep & Black Lion Mtns., Pioneer Range, 30 July 1945, C. L. Hitchcock & C. V. Muhlick 12950 (CAS, CS, DS, NY, RM, WS).

3. *Physaria pachyphylla* O'Kane & Grady, sp. nov.

TYPE: U.S.A. Montana: Carbon Co., S foot slopes of Pryor Mtns., W of Penney Peak, just N of Wyoming line on Gyp Springs Rd., barren hills of light pinkish limestone rubble, 1 July 1998, S. L. O'Kane Jr. 4511 & A. Prather-O'Kane (holotype, GH; isotypes, BRY, COLO, ISTC, MO, MONTU, NY, RM). Figure 4.

Haec species ad *Physariam spatulatam* (Rydberg) Grady & O'Kane maxime accedit, sed ab ea foliis basalibus incrassatis, pedicellis superne incurvatis atque siliqua globosa ellipsoideave distinguitur.

Perennial, loosely mounded, rosette-like growth form, caudex rarely branched, 4–7 mm thick; stems decumbent to prostrate, 2–5 cm, well exerted beyond basal leaves. Basal leaves oblanceolate to orbicular, entire, 12–20 × 4–7 mm, blade distinct from petiole, somewhat cupped, leaf tip acute, leaves nearly 1 mm thick, appearing pale green due to covering of stellate trichomes; leaf trichomes to 0.5 mm diam., 5 main rays, twice bifurcate, slightly fused near bases of main rays, terminal rays 16 to 20, rays tuberculate, appressed close to leaf surface; cauline leaves spatulate. Inflorescences racemose; pedicels curved-ascending, 5–7 mm. Sepals pale yellow, 3.5–

4 mm, pubescent; petals yellow, ligulate, 5–6 mm; styles 1–3 mm; ovary with 4 ovules per locule. Silicles globose to ellipsoid, slightly inflated, showing slight apical constriction, 3–6 × 3–4 mm, styles shorter than mature silicles; silicles pubescent, trichomes closely appressed to silicle surface.

Physaria pachyphylla (thick-leaf bladderpod) was collected and recognized as a novel taxon by O'Kane in July 1998 from the Pryor Mountain desert of Montana (Fig. 2). Further herbarium research showed that Peter Lesica collected specimens of *P. pachyphylla* in 1991; these specimens were identified as *Lesquerella alpina* var. *spatulata* (Rydberg) Payson by Rollins (Lesica, pers. comm.). This area of Montana, just north of the Wyoming border, is dry and contains a variety of edaphic conditions. Populations of *P. pachyphylla* are apparently limited to pinkish or reddish soils derived from limestone or a combination of limestone and diatomaceous earth in a small portion of the Pryor Mountain desert (ca. 60 km²) from 1300 to 1600 m above sea level. Other plants present in these dry, barren areas are compact, mat-forming perennials. *Stipa* L., *Atriplex* L., *Eriogonum* Michaux, *Phlox* L., *Cryptantha* Lehmann ex Fischer & C. A. Meyer, *Astragalus* L., *Petradoria* Greene, *Arenaria* L., and *Elymus* L. are a few of the associated grass and forb genera, while *Pinus flexilis* E. James, *Juniperus osteosperma* (Torrey) Little, and *Cercocarpus ledifolius* Nuttall are the concomitant woody species.

Other members of *Physaria* are also present in the Pryor Mountains, although not in the same vicinity as *P. pachyphylla*. The recently described *P. lesicii* (Rollins) O'Kane & Al-Shehbaz is also endemic to the Pryor Mountains, but it is found at higher elevations and is not associated with the *P. reediana* species complex (Rollins, 1995). *Physaria lesicii* is much less robust than *P. pachyphylla*, possessing thin caudices and filiform stems and pedicels. The shape of the fruiting pedicels also differentiates these taxa. *Physaria lesicii* has pedicels that are recurved in an arc, while the pedicels of *P. pachyphylla* are curved-ascending. Populations of *P. spatulata* can also be found in the Pryor Mountains, although on different soil types. The pedicels of *P. spatulata* are strongly sigmoid and much longer than the silicles; the basal leaves also are not thickened, as are those of *P. pachyphylla*. *Physaria curvipes*, while not found in the Pryor Mountains, is present in the adjacent Big Horn Mountains. The thickened leaves of *P. pachyphylla* distinguish it from *P. curvipes*.

Paratypes. U.S.A. **Montana:** Carbon Co., Gypsum Creek just N of Wyoming border, barren ridge of limestone & diatomaceous earth, pinkish white soil, 21 July 2005, S. L. O'Kane Jr. & B. R. Grady 7920 (ISTC, MO); betw. Crooked &

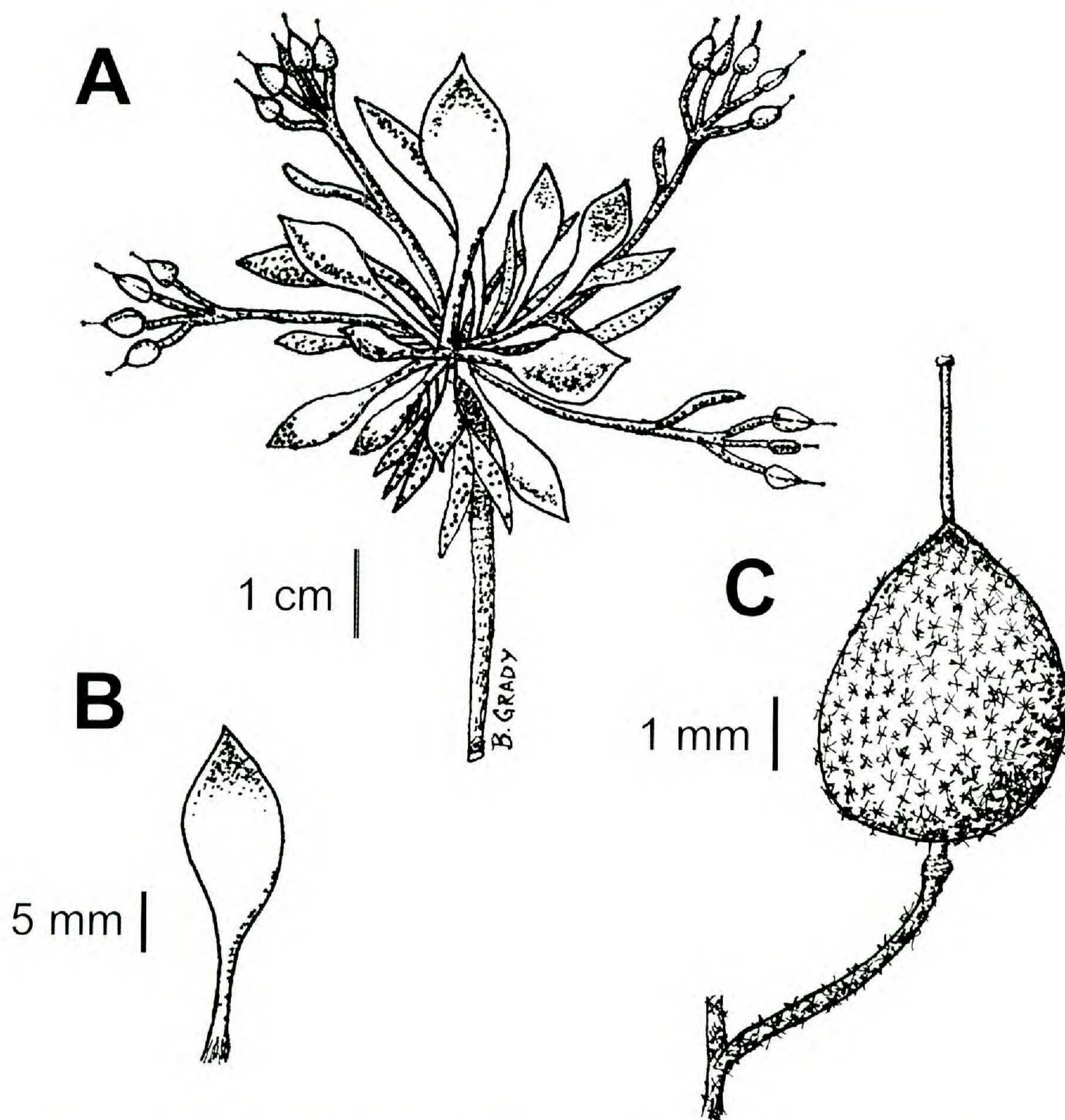


Figure 4. *Physaria pachyphylla* O'Kane & Grady. —A. Plant (pressed). —B. Basal leaf. —C. Silicle and fruiting pedicel. Drawn from the holotype, O'Kane & O'Kane 1511 (GH).

Gypsum Creeks, SSE of Penney Peak, limy-shale hills of white to reddish chip rock, 21 July 2005, S. L. O'Kane Jr. & B. R. Grady 7921 (GH, ISTC, MO, RM); betw. Layout & Crooked Creeks in foothills area at end of Sykes Ridge, gravelly red limestone-derived soil, 21 July 2005, S. L. O'Kane Jr. & B. R. Grady 7925 (GH, ISTC, MO, RM); Pryor Mtn. Desert, on a ridge above Gypsum Creek, ca. 3 mi. NW of Gyp Springs, 12 June 1991, P. Lesica 5411 (MONTU); Pryor Mtn. Desert, common on rocky limestone ridge tops on the E side of Crooked Creek, ca. 10 mi. N of Lovell, WY, 18 June 1991, P. Lesica 2608 (MONTU); Pryor Mtn. Desert, uncommon in a sandstone outcrop where road crosses small valley ca. 1 mi. N of Gyp Springs, 10 June 1991, P. Lesica 5368 (GH, MONTU); Big Horn Canyon NRA near old park entrance, aspect SE 20% slope, 8 July 1998, B. Heidel 1731 (MONTU).

4. *Physaria pycnantha* Grady & O'Kane, sp. nov.

TYPE: U.S.A. Idaho: Custer Co., on gravelly outwash mesa of limestone origin 2 mi. W of Dickey, 6400 ft., 13 June 1945, C. L. Hitchcock & C. V. Muhlick 8903 (holotype, RM; isotypes, CAS, DS, GH, MO, MONT, NY, UTC, WS). Figure 5.

Haec species ad *Physariam nelsonii* (A. Nelson) O'Kane & Al-Shebaz maxime accedit, sed ab ea foliis basalibus lineari-spathulatis, stylis brevioribus, trichomatum radiis brevioribus sed multioribus atque caule ex foliis basalibus bene exserto distinguitur.

Densely caespitose perennial forming hemispheric mounds 2.5–8 cm diam.; multicapital, caudices 3–5 mm thick; stems 2.5–7 cm, often exserted beyond basal leaves. Basal leaves entire, linear-spathulate, 15–40 × 1.5–3 mm, blade narrows gradually to petiole, appear silvery due to dense covering of stellate trichomes; leaf trichomes to 0.5 mm diam., trichome surface covered in tubercles, with 5 main rays, twice bifurcate with 16 to 24 terminal rays; cauline leaves few, spathulate. Inflorescences terminal, with 4 to 10 flowers crowded in terminal third; pedicels loosely sigmoid, 6–10 mm. Sepals pale yellow, 3–4 mm, sparsely covered with stellate trichomes; petals yellow, some with slight tinge of orange near base of petal blade, ligulate, 4–6 mm; 2

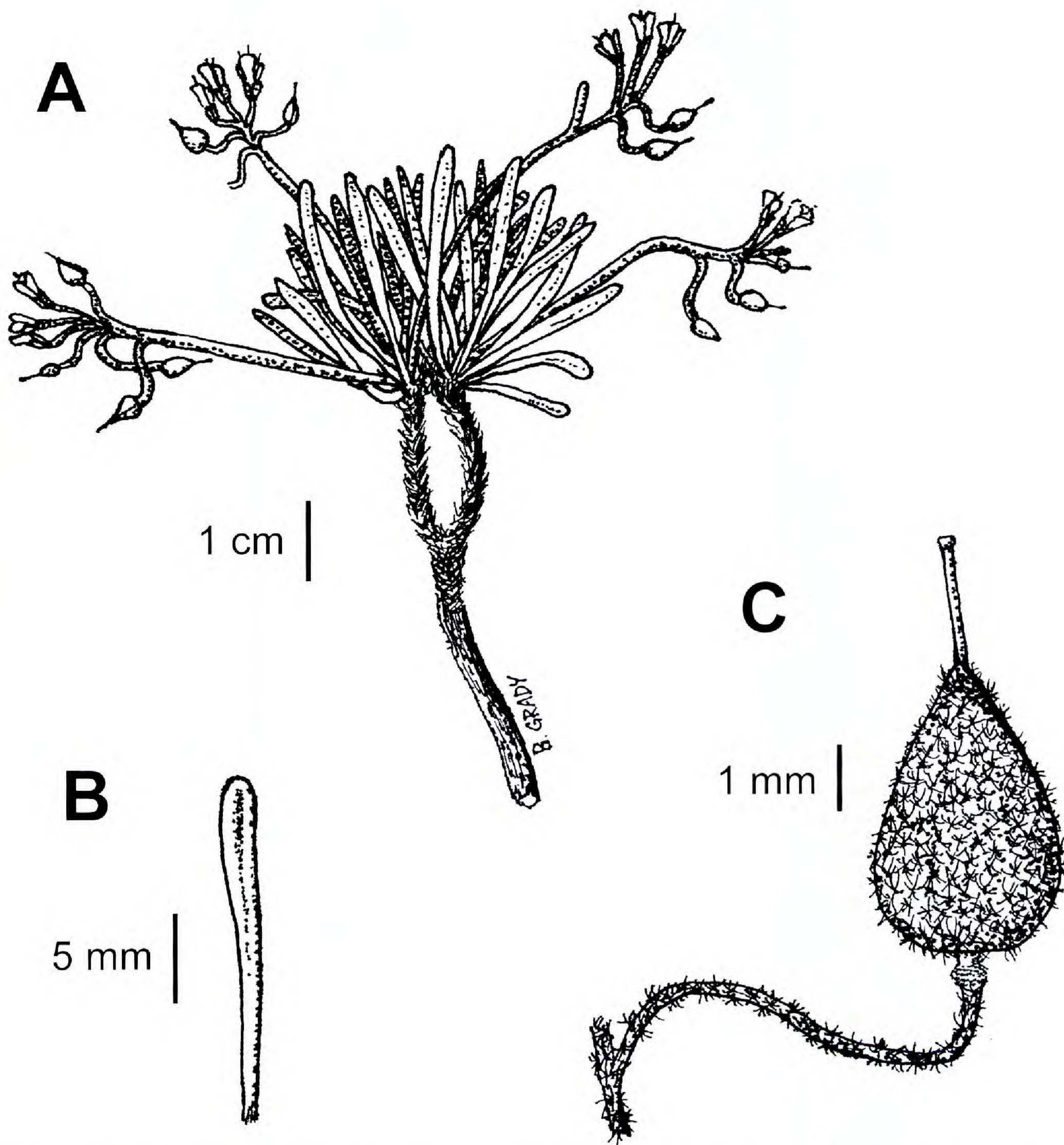


Figure 5. *Physaria pycnantha* Grady & O'Kane. —A. Plant (pressed). —B. Basal leaf. —C. Silicle and fruiting pedicel. Drawn from Grady 53 (ISTC).

or 4 ovules per locule; styles 2.5–3 mm, glabrous. Silicles ellipsoid, slightly inflated and somewhat flattened parallel to the septum, 3.5–5 × 2–3.5 mm, apex of silicles acute, mature silicles appearing slightly shaggy due to erect rays of trichomes covering silicles; styles shorter than silicles.

Physaria pycnantha (mountain-view bladderpod) occurs over a fairly broad area in east-central Idaho and southwest Montana (Fig. 2); however, populations are not evenly distributed over this range. The elevational range for *P. pycnantha* varies from 1690 to 2290 m. This mound-forming species is most often found on dry, windswept knolls, composed of gravelly substrate originating from limestone parent material.

While never a dominant member of a community, *P. pycnantha* can be abundant. It inhabits sparsely vegetated areas associated with various shrub species. *Physaria pycnantha* can be found growing with other cushion-forming plants including: *Erigeron compositus* Pursh, *Phlox albomarginata* M. E. Jones, and *Phlox muscoides* Nuttall.

Specimens of *Physaria pycnantha* were formerly identified as *P. nelsonii* (= *Lesquerella condensata*). These two species have many morphological similarities but appear not to be directly related based on the molecular phylogeny (Grady, 2005). A compact growth form, trichomes with erect rays, and loosely sigmoid fruiting pedicels are some of the traits shared by *P. pycnantha* and *P. nelsonii*. *Physaria pycnantha*

can be distinguished from *P. nelsonii* by having styles that are shorter than the mature silicles and fruiting stems that are often exerted beyond basal leaves. The styles of *P. nelsonii* are roughly equal to or exceed the length of the mature silicles, and the fruiting stems are always buried within the basal leaves. Slight differences can also be seen in the trichome morphology of the two species. The rays of *P. pycnantha* are shorter, more numerous, and fused near the bases, while the rays of *P. nelsonii* are longer, fewer in number, and not fused. *Physaria pycnantha* and *P. nelsonii* are never found in adjacent habitats, being geographically separated by more than 240 km in Idaho/Montana and Wyoming, respectively.

The northern extreme of the range of *Physaria pycnantha* is shared with that of the widespread *P. spatulata*. The features that best distinguish these two species are basal leaf shape and pubescence of the silicles. The basal leaves of *P. pycnantha* range from nearly linear to spathulate, while *P. spatulata* has basal leaves with blades that are wider and distinct from the petioles. As stated previously, the silicles of *P. pycnantha* appear shaggy due to the erect rays of the trichomes. The trichome rays are closely appressed to the surface of the silicles in *P. spatulata*. The growth form of *P. spatulata* is also more lax than the compact habit of *P. pycnantha*. The silicles of *P. reediana* have trichomes with rays closely appressed to the surface, as well as styles that are obviously longer than the silicles. The appressed trichome rays of *P. parvula* are also the discriminating trait when compared to *P. pycnantha*.

Paratypes. U.S.A. **Idaho:** Butte Co., near Hawley Mtns., side road off Pass Creek Rd., 17 mi. NNE of Hwy. 93, rocky knoll over Pass Creek, limestone gravel, 15 July 2004, *B. R. Grady 53* (ISTC); Lemhi Co., just W of Hwy. 28 near milepost 55, near Mammoth Canyon Rd., sagebrush flats and hills, clayey soil with limestone pavement, 30 June 1998, *S. L. O'Kane Jr. & A. Prather-O'Kane 4504 & 4505* (ISTC); Custer Co., Malm Gulch, ca. 12 mi. S of Challis on Hwy. 75, then 1.1 mi. E on Malm Gulch Rd., crest of sandy hill, 15 June 2004, *B. R. Grady 54* (GH, ISTC, MO, RM). **Montana:** Beaverhead Co., S of Clark Canyon Reservoir on Old Armstead Rd., 3.4 mi. NW of exit 37, Interstate 15, gently sloping hillside with scattered limestone outcrops, 16 June 2004, *B. R. Grady 58* (GH, ISTC, MO, RM); 4 mi. NW of Argenta, S end of Pioneer Mtns., cobbley roadcut of rounded alluvium with some limy rocks, 25 July 2005, *S. L. O'Kane Jr. & B. R. Grady 7947* (ISTC, MO); S toe-slope of Limestone Mtn., NNW of Dillon, limestone gravel and cobbles, 25 July 2005, *S. L. O'Kane Jr. & B. R. Grady 7949* (GH, ISTC, MO, MONT, NY, RM); S end of Pioneer Mtns., 4 mi. NW of Argenta, 15.6 air mi. WNW of Dillon, loose limy roadcut with granite and limestone gravel, 16 June 2004, *B. R. Grady 59* (GH, ISTC, MO); Lewis & Clark Co., N of Helena in saddle along gravel road to Hauser Dam, 14 May 1980, *D. J. Ramsden 527* (MONTU).

5. *Physaria spatulata* (Rydberg) Grady & O'Kane, comb. nov. Basionym: *Lesquerella spatulata* Rydberg, Contrib. U.S. Natl. Herb. 3: 486. 1896. *Lesquerella alpina* var. *spatulata* (Rydberg) Payson, Ann. Missouri Bot. Gard. 8: 210. 1921, as "*spathulata*." *Physaria reediana* subsp. *spatulata* (Rydberg) O'Kane & Al-Shehbaz, Novon 12: 327. 2002. TYPE: U.S.A. South Dakota: Lawrence Co., Black Hills, Deadwood, 5000–6000 ft., 5 July 1892, *P. A. Rydberg 534* (holotype, US; isotype, NY). Figure 6.

Perennial, loosely spreading from small (2–6 mm diam.), unbranched caudex; stems erect to decumbent, well exerted beyond basal leaves, 3–12 cm. Basal leaves erect to prostrate, inner basal leaves spathulate to oblanceolate, outer basal leaves oblanceolate to orbicular, 15–40 × 3–8 mm, blade evidently distinct from petiole, rarely folded; cauline leaves few, spathulate, evidently different than basal leaves; leaves sparsely covered by stellate trichomes; trichomes with 4 or 5 main rays, not fused, 15 to 20 terminal rays, closely appressed to leaf surface, to 0.4 mm diam. Inflorescences racemose with 6 to 20 flowers clustered on upper half of stem; pedicels strongly sigmoid, 10–20 mm, 2 × longer than silicles. Sepals pale yellow, 3.5–5 mm, pubescent; petals yellow, ligulate, 6–9 mm; styles 2.5–6 mm, usually ± equal to mature silicle length; 2 or 4 ovules per locule. Silicles various, lanceolate to globose, slightly inflated, (2.5–)3–6 × 2–3.5 mm, usually strongly narrowed at apex, silicle trichomes sparse, closely appressed to surface.

Physaria spatulata (spatula-leaf bladderpod) was first described by Rydberg in 1896 from the Black Hills of South Dakota. At various times it was recognized as an intra-specific taxon of *P. reediana* (= *Lesquerella alpina*) or as a variant form of that species undeserving of taxonomic rank (Payson, 1921 [1922]; Rollins & Shaw, 1973). We believe *P. spatulata* to be a distinct taxon worthy of specific rank. Besides obvious morphological differences, *P. spatulata* and *P. reediana* are not directly related based on recent molecular studies (Grady, 2005). This unexpected result is counter to the previous taxonomic treatments of the two species (Payson, 1921 [1922]; Rollins & Shaw, 1973; Rollins, 1993).

Physaria spatulata has a broad geographic distribution and grows at a variety of elevations. It is found in the western counties of Nebraska, South Dakota, and North Dakota, extending west through the northern half of Wyoming, throughout most of Montana, and north to the southern extremes of Saskatchewan and Alberta (Fig. 2). While *P. spatu-*

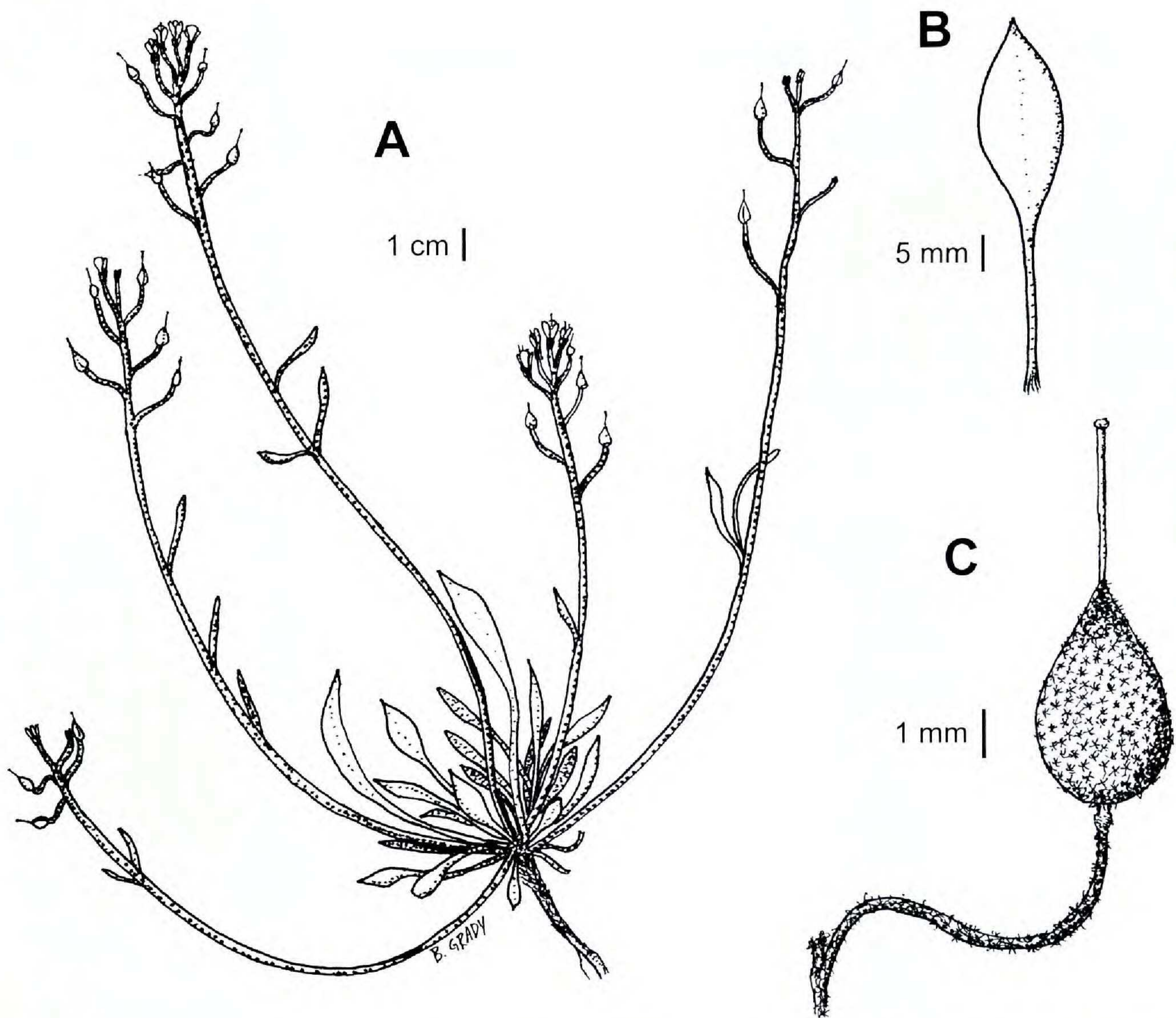


Figure 6. *Physaria spatulata* (Rydberg) Grady & O'Kane. —A. Plant (pressed). —B. Basal leaf. —C. Silicle and fruiting pedicel. Drawn from *Grady 71* (ISTC).

lata is most commonly found in grasslands at elevations from 900 to 1525 m, some populations are present in sub-alpine communities of northern Wyoming and southern Montana up to 2900 m in elevation. High levels of intraspecific variation seem to correspond to these wide geographic and altitudinal ranges. In general *P. spatulata* is a loosely spreading plant, although some exceptions are notable. When found at elevations above 2290 m, it has a more caespitose growth form with a thickened caudex, and the fruiting stems exceed the basal leaves in length. The higher-altitude localities are found in mountain ranges such as the Absorka, Beartooth, and Pryor Mountains along the border between Wyoming and Montana. Some specimens here have basal leaves that are narrower than those usually found in other areas. The typical outer basal leaf of *P. spatulata* is broadly spatulate with an acute apex. The blade is clearly distinguished from the petiole. Some specimens of *P. spatulata* have narrowly spatulate basal leaves, lacking wider blades (most notably some populations from central Montana), but still obviously represent

this taxon, based on pedicel and silicle morphology. Silicle shape can also vary somewhat in *P. spatulata*, even among populations. Apical compression is usually evident, and compression parallel to the septum is common. The silicles are usually longer than wide. Although not common, some specimens have been observed to have sub-globose fruits, but these clearly represent variations in form within the species.

Physaria spatulata differs in a number of ways from *P. reediana* and their ranges show little overlap. The growth form of *P. reediana* is more compact than that of *P. spatulata*. *Physaria reediana* has lanceolate basal leaves and styles that are longer than the mature silicles (3–5 mm) and are bent or curled near the stigma. *Physaria spatulata* most closely resembles *P. curvipes*, although their fruit morphologies are different (Figs. 1, 6). *Physaria montana* (A. Gray) Greene is found in mountainous areas in the southern portion of the range of *P. spatulata*. The two species are distinct in that *P. montana* has ellipsoid silicles and cauline leaves that are secund. *Physaria ludoviciana* (Nuttall)

O'Kane & Al-Shehbaz has a broad range that overlaps the range of *P. spatulata* in many areas. Recurved pedicels and involute inner basal leaves separate this taxon from *P. spatulata* (Rollins & Shaw, 1973). Another species that could be confused with *P. spatulata* is *P. lesicii*, which is only known from the Pryor Mountains of southern Montana. The fruiting pedicels of *P. lesicii* are recurved, and the silicles are globose (Rollins, 1995).

Representative specimens examined. CANADA. **Alberta:** bluffs of N fork of Milk River, 3 mi. E of Whiskey Gap, *R. C. Rollins* 57212 (B, BM, CAS, GH). **Saskatchewan:** vicinity of Killdeer, 6 mi. N, NE 1/4 6-3-III W 3rd, dry slope of roadcut, soil buff, calcareous silt of Ravenscarg, *J. H. Hudson* 2341 (COLO, DAO, ISTC). U.S.A. **Montana:** Carbon Co., near S end of Sykes Ridge, E Pryor Mtn., windswept fellfield, *S. L. O'Kane Jr. & B. R. Grady* 7924 (ISTC, MO); Beaverhead Co., S of Dewey, 1 mi. S on road to Quartz Hill Gulch, roadside on steep hill of limestone gravel, *B. R. Grady* 60 (GH, ISTC, MO, NY); Choteau Co., White Cliffs area, "Steamboat Rock Landing," in sand and mudstone cliffs, *K. H. Lackschewitz* 11660 (GH, MONTU). **Nebraska:** Sioux Co., rocky grassland W of Harrison, *W. Kiener* 20482 (NEB). **North Dakota:** Billings Co., eroded prairie pasture hillside, 1/2 mi. S, 6 mi. W of Fryburg, dry rocky gravel clay soil, *S. Stephens & R. Brooks* 40276 (WIS). **South Dakota:** Custer Co., limestone ridge of Black Hills, 27 mi. W of Custer, July 1950, *H. D. Ripley & R. C. Barneby s.n.* (GH). **Wyoming:** Campbell Co., 9.1 mi. N of Gillette along Hwy. 59, just N of railroad overpass, loose red gravel at base of rocky outcrop, *B. R. Grady* 71 (GH, ISTC, MO, RM).

Acknowledgments. We are indebted to Victoria C. Hollowell and Ihsan Al-Shehbaz for their valuable

comments and recommendations on the manuscript. We thank James C. McKeown for his advice regarding the Latin diagnoses. Thanks are also in order for the curators and directors of the cited herbaria for the loans of material.

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